The Population Consequences of Polygyny in the Ant *Leptothorax curvispinosus*[1]

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ABSTRACT

In colonies of the ant, *Leptothorax curvispinosus* Mayr, the number of eggs in the standing crop appears to increase principally with the number of queens, but the number of larvae, and hence the colony growth rate, is independent of the number of queens, depending instead primarily on the size of the worker population. Hence the average reproductive potential of individual queens falls off linearly with an increase in their number. On the other hand, the presence of supernumerary queens lengthens the survival time of colonies. The latter circumstance alone, if combined with a higher degree of genetic relatedness among coexisting queens, counteracts the lowered per-queen reproductive potential and could be sufficient to favor polygyny in natural selection.

The occurrence of multiple fertile queens within single colonies (polygyny) has a scattered phylogenetic distribution within the ants, evidently having arisen repeatedly and independently in evolution. It occurs in species as primitive as *Amblyopone australis* and is widespread as a minority phenomenon in the dominant subfamilies Ponerinae, Myrmicinae, Dolichoderinae, and Formicinae (reviews by Hölldobler 1962, Buschinger 1967,[2] Baroni-Urbani 1968, and Wilson 1971). Not all such cases represent completely functional polygyny in the sense that multiple queens lay eggs while living side by side. Virtually all transition stages have been documented between obligatory monogyny and functional polygyny. The following sequence incorporates the terminology of Hölldobler and Buschinger:

1. *Obligatory monogyny.* Only one laying queen can exist in a nest; supernumerary queens are eliminated either by the dominant queen or by the workers.
2. *Oligogyny.* More than one queen can occur in a nest, but only when they remain well apart from each other.
3. *Functional monogyny.* Multiple, inseminated queens occur, but only one lays eggs.
4. *Pseudopolygyny.* Some dealated queens are present that are not inseminated but instead serve as workers; these individuals may or may not occur in addition to supernumerary laying queens.
5. *Polygyny.* At least two laying queens live closely together in the same nest.

This report is concerned with true polygyny. The question of greatest interest is the adaptive significance, if any, of the phenomenon. It is proposed to learn whether the coexistence of multiple laying queens alters the survivorship and productivity of colonies in a way that enhances the inclusive fitnesses of the queens. A subsidiary problem is whether the competition of queens affects the stability of numbers of various life stages. It is conceivable that colonies find it difficult to maintain optimal brood-worker ratios with multiple queens contributing to the egg pile and perhaps interacting with each other in unsuspected ways. These questions can be answered only through demographic analysis.

PROCEDURE

Colonies of *Leptothorax curvispinosus* Mayr were obtained from the E. S. George Reserve, near Pinckney, Mich., and cultured in simple artificial nests consisting of 10-cm-long glass tubes with internal diameters of 5 mm. The tubes were plugged at one end with moist cotton balls and left open at the other end to permit workers to forage outside. Each one containing a colony was placed on the floor of a clear plastic dish small enough in turn (9×15 cm on the side by 6 cm deep) to be placed on the stage of a dissecting microscope. It was then possible to make full censuses of all life stages at regular intervals without disturbing the colonies. During a period of 3 months the behavior of the queens of 3 polygynous and 6 monogynous colonies were recorded in some detail; at the same time censuses were taken at intervals of 8 days or less. Two of the polygynous colonies contained 3 queens and one had 2 queens. Additional polygynous and monogynous colonies were censused on single occasions.

Voucher specimens from the colonies have been deposited in the Museum of Comparative Zoology, Harvard University.

RESULTS

Two of the polygynous colonies, one containing 3 queens and the other 2 queens, were observed for a total of somewhat more than 100 h over a period of one month, with particular attention being paid to oviposition. During this time all the queens laid eggs, with none being conspicuously more productive than others. Their interactions were nearly neutral. In most instances they moved around each other as if encountering inanimate obstacles, or else moved slowly away for very short distances. There was neither attraction nor strong avoidance. Nevertheless, a subtle form of reproductive dominance occurred. In both nests, one of the queens handled the freshly laid eggs of others more roughly than their own were handled, sometimes going so far as to rupture and to eat them. Eggs produced by one of the queens in the trigynous colony were consistently destroyed in this manner by the "dominant" queen. Thus, although multiple queens were contributing

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[2] Buschinger, A. 1967. Verbreitung und Auswirkungen von Mono- und Polygynie bei Arten der Gattung *Leptothorax* Mayr (Hymenoptera: Formicidae). Ph.D. Dissertation, Bayerischen Julius-Maximilians-Universität zu Würzburg, Germany. vii + 115 pp.

eggs to the brood pile, their net production was less than if they had been laying singly at the same rate. Furthermore, direct observations have shown that the queens compete exploitatively for food to at least a limited extent. Such interaction might reduce the oviposition rate somewhat; the possibility has not been tested by experimentation. (A more detailed account of these aspects of behavior is presented by Wilson [1974].)

The census data, most of which are presented in Fig. 1–4, were subjected to graphical and multiple regression analysis, permitting the following conclusions to be drawn:

1. The absolute and relative numbers of all brood stages fluctuate widely. However, the amplitude of fluctuation does not differ between monogynous and polygynous colonies (Fig. 1–2). Thus the irregularities introduced into polygynous colonies by contributions from multiple egg-layers and competition between them are not translated into noticeable changes in amplitude.

2. The number of pupae has no discernible effect on the numbers of eggs or larvae. It is too low, and the data too variable, to test its relation to the numbers of queens or workers.

3. The number of eggs appears to increase strongly with the number of queens; it increases slightly with the number of workers while decreasing slightly with the number of larvae. The estimated relation based on an assumption of linearity is the following:

(No. of eggs) = 16.206 + 5.667 (no. of laying queens) + 0.325 (no. of workers) − 0.552 (no. of larvae)

The worker and larva coefficients in the above equa-

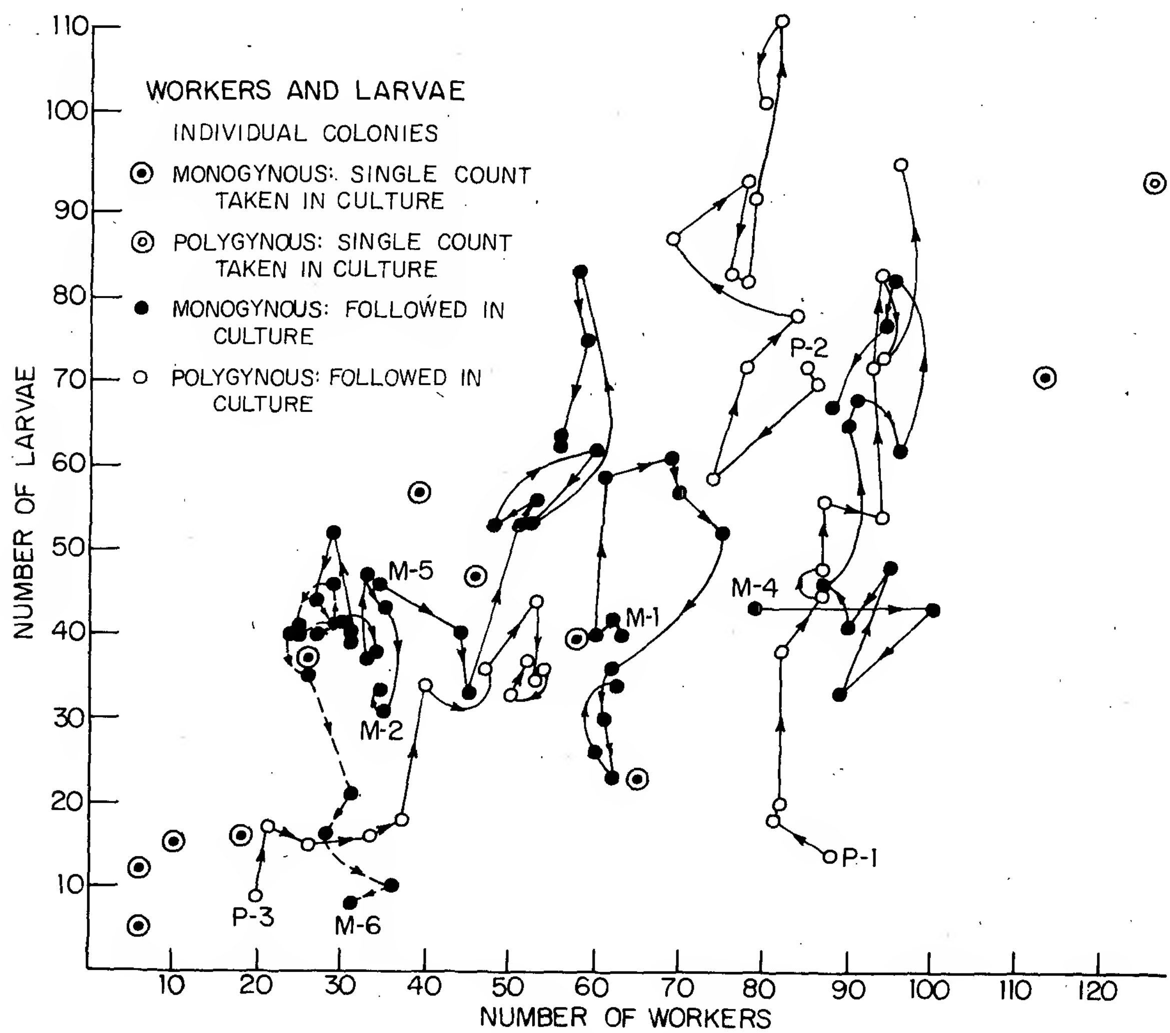

FIG. 1.—The relation between the number of workers and the number of larvae in individual colonies of the ant *Leptothorax curvispinosus*. Polygynous colonies are indicated by open circles, monogynous ones by closed circles. Colonies censused only on a single occasion are further indicated by an enclosing circle. Others were counted at 8-day intervals over a 3-month period, and their progress through time is tracked in this figure by arrows. Numbers refer to code designations of colonies.

tion are significantly different from zero at the 99.9% and 99.7% confidence levels, respectively. The confidence level of the queen coefficient is only 85%. If it is accepted as significant, as suggested by direct observations of the egg-laying process, the simplest hypothesis is that the number of eggs in the standing crop increases linearly with the number of queens. The standard error of the coefficient is 3.75.

4. The standing crop of larvae does not vary significantly with the number of laying queens. It increases with the number of workers and decreases with the number of eggs. The estimated relation based on an assumption of linearity is the following:

(No. of larvae) = 23.84 + 0.567 (no. of workers) − 0.744 (no. of eggs)

The coefficients are significant at the 99.9% and 99.7% confidence levels, respectively. The inverse relation between the standing crop of eggs and larvae is similar to findings in the myrmicine genus *Myrmica* and in the army ants (see Brian 1965, Schneirla 1965).

5. The standing crops of both eggs and larvae display the "reproductivity effect" which has been previously recorded in the social wasps and bees (Michener 1964, Wilson 1971). This means that, although the absolute numbers of these immature stages increase with the size of the worker population, the numbers *per worker* decrease. The productivity is raised at the colony level while being lowered at the individual level.

DISCUSSION

The results of this study establish that over a wide range of colony size the chief correlate of colony growth is the number of workers. The number of laying queens appears to make no difference. Polygyny may be associated with larger colony size, as Buschinger (1967)[2] documented for *L. acervorum* and other polygynous species in Europe, but cause and effect is evidently the reverse of what might have been expected intuitively. In other words, larger colonies are more likely to become polygynous; they did not become large just because they were initially polygynous.

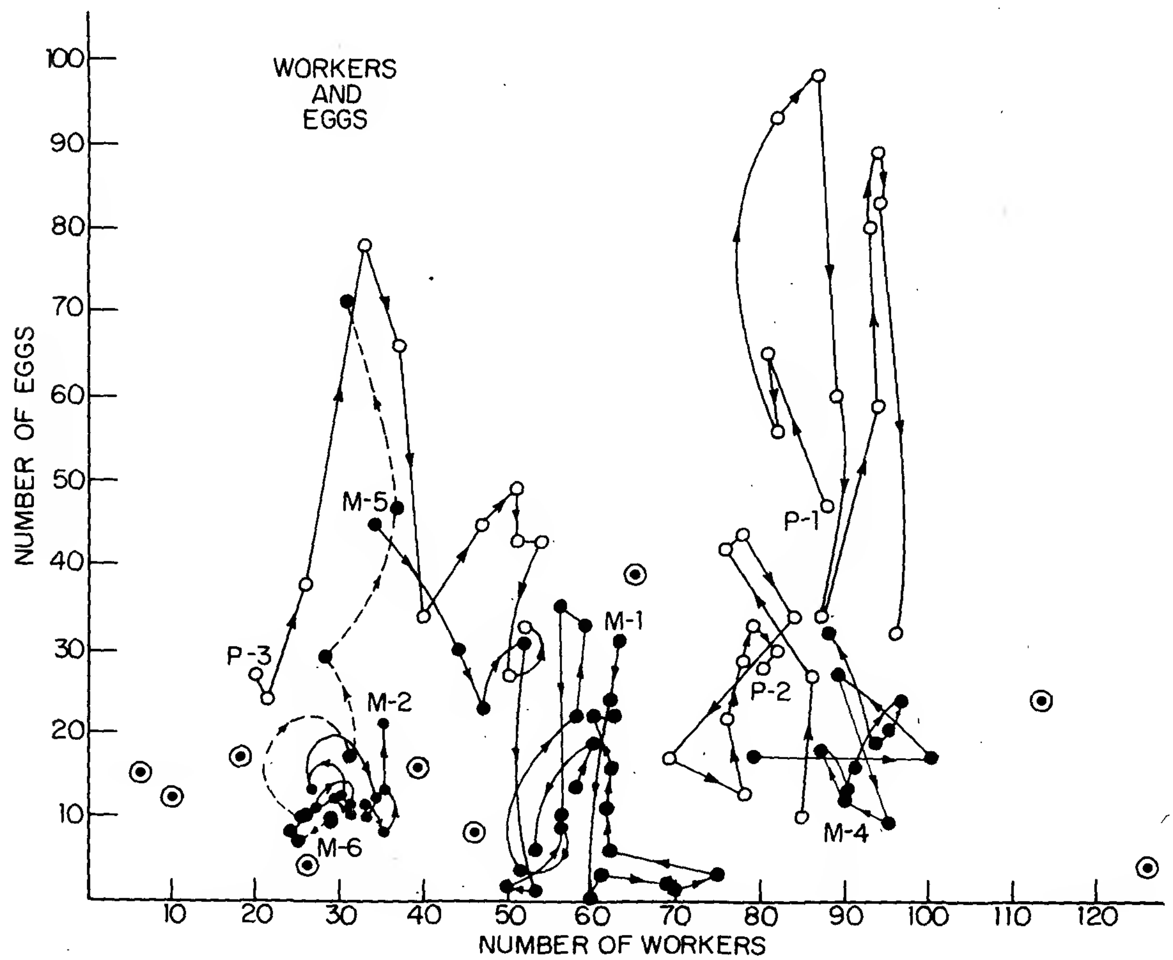

FIG. 2.—The relation between the number of workers and numbers of eggs in individual colonies of *L. curvispinosus*. Conventions as in Fig. 1.

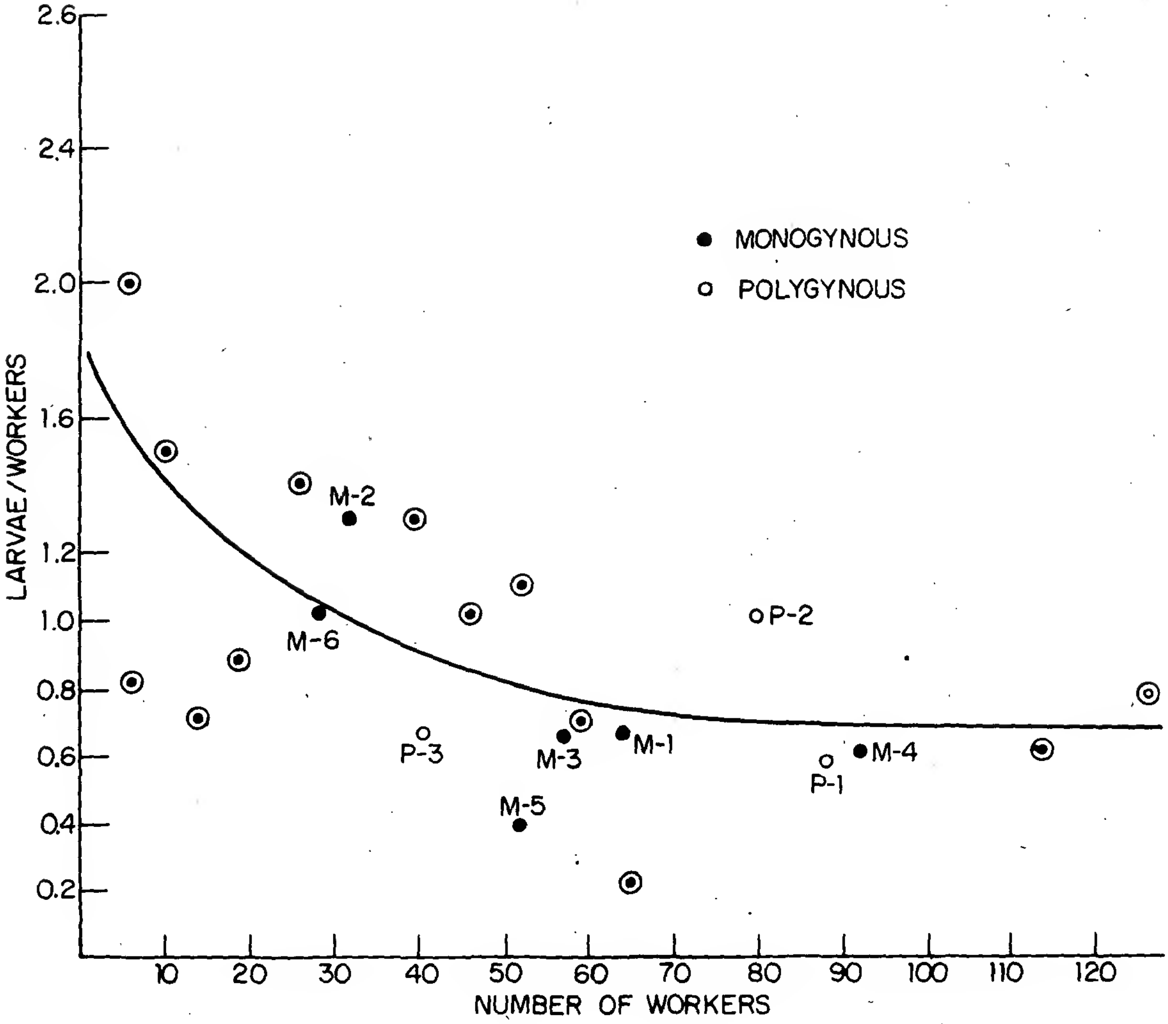

FIG. 3.—The relation between the standing crop of larvae per worker and the number of workers in individual colonies of *L. curvispinosus*. Conventions as in Fig. 1, except that the census points given for the tracked colonies are the averages taken over the 3-month period.

In fact, membership in polygynous colonies holds some marked disadvantages for the queens. The average yield of offspring per queen is reduced to the reciprocal of the number of egg-laying queens present. Thus when 2 queens are present, the per-queen productivity is reduced to ½, 5 queens reduce per-queen productivity to ⅕, and so on. Buschinger (1967) found that in *L. acervorum*, polygynous colonies produced fewer winged reproductive queens and males than did monogynous colonies. If this inequality also holds for *L. curvispinosus*, it exacerbates the genetic disadvantage of belonging to a polygynous colony in that species.

How can polygyny evolve when it imposes such handicaps? Two advantages conceivably exist that counteract, and perhaps outweigh, the costs just cited. First, multiple queens prolong the life of the colony as a whole. Among numerous *L. curvispinosus* colonies maintained in the laboratory but not included in the population study, 6 monogynous colonies lost their queens over a period of several months. None continued to produce new workers. Two digynous colonies lost one queen; the remaining queen sufficed in each case to maintain a high rate of new worker production. If the multiple queens are related to one another, there could be a sufficient gain in inclusive fitness through prolonged colony life to make mutual tolerance adaptive. Should the queens prove to be no more closely related than queens sampled from monogynous colonies, this hypothesis will fail. The second advantage might accrue at the time of early colony growth. Laboratory experiments on *Lasius flavus* (F.) (Waloff 1957) and *Solenopsis invicta* Buren (Wilson 1966) have shown that queens starting nests cooperatively survive longer and rear more workers per queen in the first brood than those

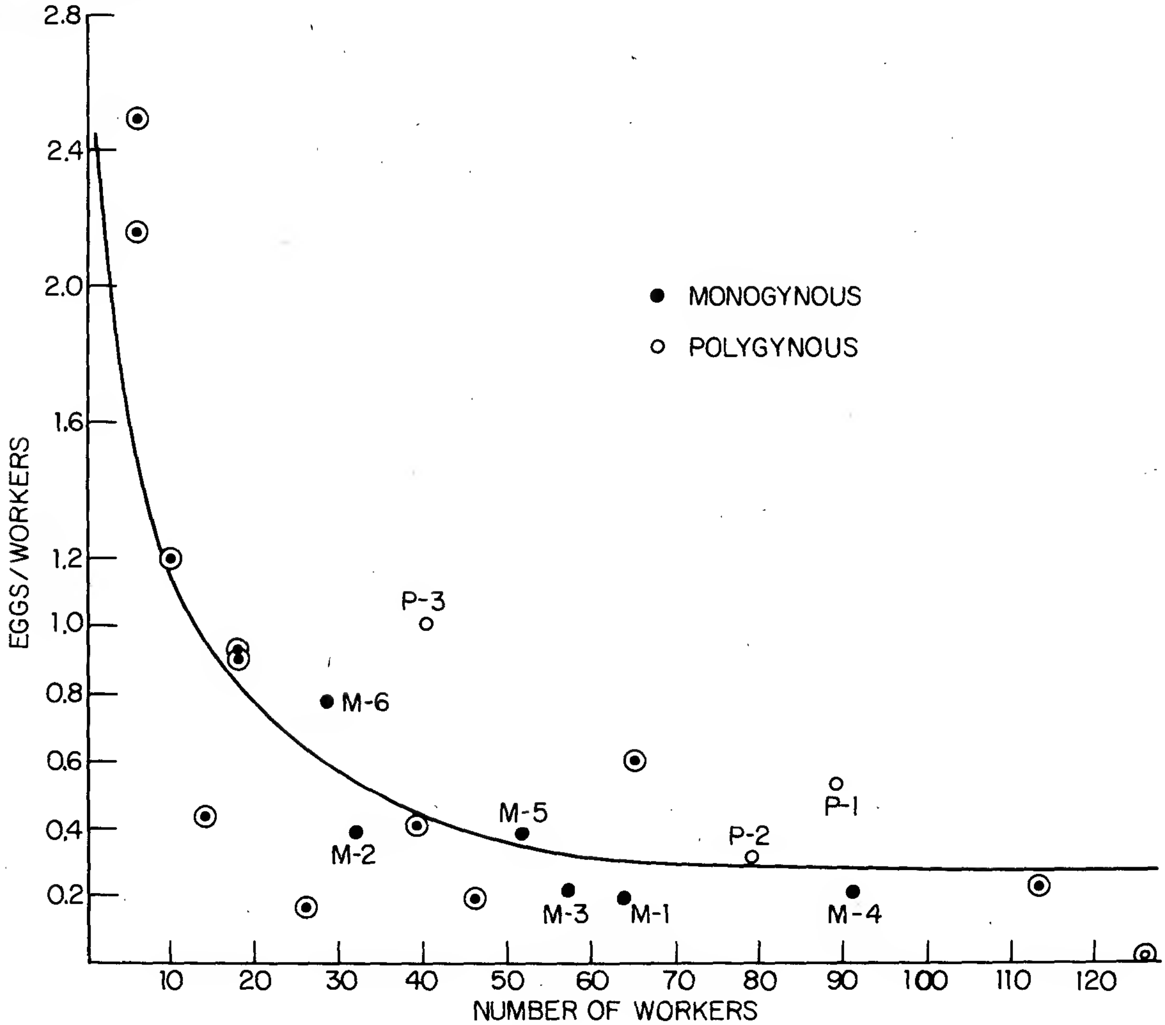

FIG. 4.—The relation between the standing crop of eggs per worker and the number of workers in individual colonies of *L. curvispinosus*. Conventions as in Fig. 1, except that the census points given for the tracked colonies are the averages taken over the 3-month period.

that found colonies singly. *Leptothorax curvispinosus* queens sometimes start nests cooperatively (T. Alloway, personal communication). It is possible that such groups offer superior individual survival value, and that many of the ultimately larger polygynous colonies are started in this way. Talbot's censuses taken through one summer revealed the interesting fact that the percentage of polygynous colonies in the E. S. George Reserve population increased steadily through the season: June, 3.4%; July, 3.7%; August, 7.5%; September, 10.0% (Talbot 1957). This result could be due either to the greater survival rate of polygynous colonies or the adoption of queens by established colonies following the nuptial flights, which began in early July.

The hypothesis is proposed here that the advantages outweigh the disadvantages, favoring polygyny in *L. curvispinosus*. But conditions do not insure universal polygyny within the species. The basic pattern of colony reproduction by nuptial flights has been preserved, with the result that many colonies are founded by single queens. Those colonies founded by multiple queens survive longer, both at the time of founding and at later stages of growth, with the result that larger colonies have a higher frequency of polygyny than small ones. The effect is due to differential colony survival rather than to differential colony growth.

ACKNOWLEDGMENT

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